NOTES ON THE FEEDING AND BREEDING BEHAVIOUR OF *GYMNOPLEURUS GEMMATUS* HAROLD AND *GYMNOPLEURUS MILIARIS* (F.) (COLEOPTERA: SCARABAEIDAE)[1]

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(With a text-figure)

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Field studies on the feeding, mating and competitive behaviour of *Gymnopleurus gemmatus* and *G. miliaris* were conducted in Bangalore. Both the species were diurnal and fed both at the pat and on dung balls that they fashioned, transported and buried before feeding. Competition was intense both for dung balls and mates within the species and for dung balls alone between the species. Species belonging to the genera *Onthophagus* and *Caccobius* were found frequently as kleptoparasites in the brood balls of these beetles.

Introduction

Gymnopleurus, a dung rolling coprophagous genus of beetle, is widely distributed in Asia, Europe and Africa (Arrow 1931). The fashioning and transportation (by rolling) of dung balls, by these beetles not only reduces congestion at the resource site but could also give the rollers a competitive edge over the dung burying groups like the Coprini, Onthophagini, Onitini, etc., which compete for food and burial space beneath and around each dung pat (Halffter and Matthews 1966).

It was Fabre (1897), the famed french naturalist, who made the first systematic studies of the three dung rolling genera *Scarabaeus, Gymnopleurus* and *Sisyphus.* Subsequently, several studies on the ball making, rolling and burial behaviour of *Gymnopleurus* have been made (Hingston 1923, Honda 1927, Prasse 1957a, 1957b, 1957c, 1958a and 1958b).

In India, however, after Hingston (1923), the behaviour of these beetles (in particular *Gymnopleurus*), has gone largely unnoticed. A study on the field behaviour of two commonly occurring species of *Gymnopleurus*, namely *G. miliaris* and *G. gemmatus* was therefore undertaken.

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Material and Methods

The feeding and breeding behaviour of *G. miliaris* and *G. gemmatus* were studied in grazing fields at two locations (Hebbal and Allalsandra) on the outskirts of Bangalore (12° N lat. and 77° E long., 916 m alt.) in S. India. The study sites are situated at about 7 and 11 km north of Bangalore, respectively. The rainy season which commences here in late April continues till the end of September during which period these beetles are active. During the period of study (1984-1986) the mean maximum and mean minimum temperatures were 29.8° C and 18.2° C while the total annual rainfall amounted to 548.3 mm.

Observations were made on the following elements of beetle behaviour, namely a) approaching food, b) feeding, c) ball making, d) ball rolling, e) mating, f) intra- and inter-specific competition, and g) kleptoparasitism.

The rollers, *G. miliaris* and *G. gemmatus* were identified by Dr. R. Madge of the British Museum (Natural History), London.

Results and Discussion

The beetles commenced activity after the first rains in late April. They are diurnal, with their period of activity usually extending from 0700 to 1830 hrs. Light showers did not make them cease activity.

Approach to food: The beetles always located

their food by flying low, in a zigzag manner and alighting at a mean distance of 8.65 cm (*G. gemmatus*) and 8.85 cm (*G. miliaris*) from the food source. Whenever they landed on their backs they used their mid pair of legs as pivots to right themselves. A few alighted directly on the dung pat. Having detected the presence of food, the beetles, with antennae waving feverishly, walked briskly towards it. On reaching the food source, they walked all over it to finally select a suitable spot to commence feeding.

Feeding: Both the species of *Gymnopleurus* were attracted to human faeces, sheep excrement and cow dung. It was visually apparent that the beetles preferred human faeces of the three sources of excrement.

The beetles commenced feeding at the dropping after having selected a suitable spot on the dung mass. When feeding on sheep-pellets, it was noticed that the beetles fed exclusively in the inner core by boring into the pellet. This brief period of feeding was followed by ball making.

Balls of excrement were fashioned for various purposes, namely i) for food, ii) as nuptial gifts, and iii) for rearing brood.

Both the species of *Gymnopleurus* made food balls, rolled, buried and fed on them unlike *G. mopsus* Pallas and *G. geoffroyi* Fuessly (Prasse 1957a, 1957b, 1958a) which never made any food balls. Hingston (1923) also reports food ball preparation in *G. miliaris*.

Prasse (1957a) has reported that species of *Gymnopleurus* undergo a 'Reifungsfrass' period of 3-3.5 months. In the present study the beetles which emerged with the onset of the rains were found mating on the first day and brood balls were made a week after. So the Reifungsfrass period is definitely shorter for these two species of *Gymnopleurus*.

Ball making: After selecting a suitable spot on the faecal mass the beetles carved out circular segments of dung from the rest of the mass using their front tibiae and clypeus. During the process of fashioning, bits of dung were added from the main mass whenever the initial mass was found to be inadequate.

The sphere was finally detached from the main mass by the beetle moving down the side of the ball to its point of attachment at the base. The beetle then pushed against the ball with its middle and hind pairs of legs till the ball got detached. It was then rolled to the edge of the pat.

Perched on the ball they patted it into a smooth sphere using their fore tibiae. Once again, any deficiency in the quantum of dung making up the sphere was made up by adding from the main mass and if in excess, the extra material was cut away with the clypeus and discarded. Each beetle took about 11.07 ± 1.03 min. (*G. gemmatus*) and 10.10 ± 1.23 min. (*G. miliaris*) to construct and fashion one ball. In those cases where the partner was chosen during the period of ball construction, the new partner also helped in ball making.

When sheep pellets were used as raw material for making balls, a different technique was adopted. The beetles then broke open a number of sheep pellets to collect sufficient material from the soft inner core. These were then used sequentially in the fashioning of a ball of requisite proportions.

Ball making was observed at temperatures between 23.3°C and 29.4°C.

Ball rolling: The ball of dung once detached was rolled away from the dung pat to a distance of about 10-20 cm, where the beetle was generally noticed to finally shape the ball. Sitting on the ball, the beetle patted the ball into shape using its forelegs, as well as by intermittently pressing the ball with its clypeus. On completion of this final fashioning of the ball into a compact spheroid the beetle began rolling the ball. The average diameter and weight of the balls rolled by a lone beetle was 1.0 ± 0.13 cm and 0.34 ± 0.11 g (*G. gemmatus*), 1.03 ± 0.1 cm and 0.36 ± 0.09 g (*G. miliaris*). On the other hand, when pairs rolled the ball, it was 11.15 ± 0.11 cm and 0.36 ± 0.06 g (*G. gemmatus*), 1.13 ± 0.31 cm and 0.48 ± 0.03 g (*G. miliaris*).

As the ball was rolled along, it acquired a thin coating of soil. If a single beetle was engaged in rolling, it pushed the ball with its middle and hind pairs of legs while it had its forelegs on the ground. In 90% of the cases it was the male that made the

ball; to be later joined by the female. As Thornhill (1983) suggests, the "material benefits" — here the dung ball — are provided by males probably to reduce the loss of energy in the female in making a ball as she has to spend a lot of energy on other activities like — rolling, burying and brood ball making, egg laying, etc.

However, it was noticed that the maker of the ball, irrespective of its sex, did not readily accept as a partner the first individual that came up to the ball. If a male was the ball maker it fought and chased away all approaching males; while it accepted an approaching female, only after a brief combat of about 15-20 seconds. If the ball maker was a female it too chased away all females but accepted a male after a brief combat. To ascertain the sexual identity of each rolling pair, over 50 pairs of both *G. gemmatus* and *G. miliaris* were dissected. Almost every pair, it was found, consisted of a male and a female. In only two instances members of the same sex were found rolling the ball.

This was the result of intra-sexual combat in which individuals of the same sex fought each other in a bid to steal and gain possession of the ball. In fact, females of both the species were rolling a ball. This behaviour has been reported earlier for *Scarabaeus sacer* (Fabre 1897) and *G. miliaris* (Hingston 1923). In transporting the ball, males and females took up characteristic stances in all cases. The female always stood behind the ball, pushing with the last two pairs of legs, while the male pulled the ball from the front using its last two pairs of legs.

This contradicts Hingston's (1923) observation that 'as a rule' the male pushes the ball while the female pulls it. Observations similar to that in the present study were made by Honda (1927) for *G. sinuatus* (Ol.) and Prasse (1957b, 1958a) for *G. mopsus* and *G. geoffroyi.*

During the course of rolling the male was unable to keep pace with the female. He would tumble off but the female would continue rolling, apparently unconcerned, while the male hastened to catch up. On the other hand, in cases where the female fell, the male waited with the ball for her to rejoin him. He would permit her to resume her role only after a short skirmish lasting 2 to 3 seconds. If, for some reason, the female failed to return, the male abandoned the ball after a period of waiting. In one instance the male waited for 3 min. 40 sec. and in another for 5 min. during which time they met new females with whom they continued the activity of rolling. Unlike males the females continued rolling the ball and buried it even when the males had deserted.

In some cases, the male was found sitting on the side of the ball instead of pulling it, which contradicts Hingston's (1923) report that this is found only in *Scarabaeus sacer* and never in *G. miliaris.* Nevertheless Prasse (1957b) has reported the same for the two species of *Gymnopleurus.* In such cases the male would get off the ball when the female needed help in surmounting an obstacle.

The beetles never rolled the ball in a straight line. Most were found rolling the ball in a haphazard manner, sometimes crossing the same spot several times and finally burying their balls close to the starting point, even though the balls were rolled for much greater distances than the shortest distance between the food source and the burial site. This once again contradicts Hingston's (1923) observations that the pellets must be rolled strictly in straight lines.

Whenever the beetles encountered an obstacle they adopted any one of the following three strategies. i) crossed over the obstacle, ii) took a detour, or iii) buried the ball at the base of the obstacle.

The average distance rolled by a pair of beetles was 11.71 m, n = 15 (*G. gemmatus*) and 22.22 m, n=15 (*G. miliaris*). The average distance rolled per minute was 105.10 cm, n=15 (*G. gemmatus*) and 119.53 cm, n = 15 (*G. miliaris*). When a single beetle rolled a ball it often stopped rolling, climbed on the ball, checked all around the ball and got back into position to continue rolling the ball. On the other hand when a pair were engaged in ball rolling, the female stopped periodically to inspect the surface of the ball. On encountering the male on the other side she often tried to butt him off, only to recognize him later and then continue rolling. The average time taken for rolling was 16 min., n = 10 (*G. gemmatus*)

and 20 min., n = 10 (*G. miliaris*).

Ball burying: In burying the ball, individuals and pairs adopted different strategies. In the case of pairs, it was always the female who selected the burial spot. She walked away from the ball, examined a certain area and then returned. When individual beetles were involved, they tested and selected sites while holding onto the balls with their hind legs.

Selecting a suitable burial site involved the prior rejection of a number of sites. Four such rejected sites were examined by digging. Strangely, the kleptoparasites *Onthophagus pygmaeus* (Schall.) and *O. centricornis* (F.) were found to be present beneath the soil surface.

When single beetles buried balls they came out of their pits several times during the process of digging to check for the presence of the ball. Having made a small pit, the beetle dragged the ball into the pit and disappeared beneath it to continue digging as a result of which the ball disappeared into the soil.

In case of pairs, it was always the female which took to digging while the male stood guard. After making a small pit, she rolled the ball with her hind pair of legs. Sometimes the male helped her in pushing the ball into the pit. During the period of burying the male either sat on the ball or walked around the pit. Sometimes he held the ball with his front two pairs of legs while he stood at the rim of the pit. When 75% of the ball disappeared into the soil, the male also entered the soil to join the female. The average time required for burying the ball was 14.36 ± 4.06 min., n = 10 (*G. gemmatus*) and 13.45 ± 2.08 min., n = 15 (*G. miliaris*).

Digging up twenty marked burial sites after a day or two revealed the following.

1. During the early part of the season, most of the lone beetles used the balls for feeding and only frass and faecal matter were found in the burrow.

2. Later in the season, lone females used the ball for raising brood.

3. Balls rolled by the pairs used them both for enticement and raising brood.

Mating: Both species generally mated in the space between the side of the dung ball and the pit and sometimes above the ball when it had fully descended into the pit. The male then clasped the female in the copulatory position, and kept strumming on the female's elytra with its forelegs. The frequency of strumming increased whenever other insects moved in the vicinity. The female generally fed on the dung ball while engaged in mating, while at times she stood still doing nothing. On completing mating which took about 13 min., n = 4 (*G. gemmatus*) and 19 min. 30 sec., n = 5 (*G. miliaris*), the male stayed with the female for a further 4-5 sec., after which time it either flew away or stayed on to guard the female when he suspected the presence of other males. The female continued digging beneath the dung ball. Some pairs of beetles (3 of *G. miliaris* and 2 of *G. gemmatus*) were seen mating even before the pit was dug, such beetles abandoned the ball and flew away.

Occasionally males were found trying to mate on the dung pat, but were not successful.

Brood ball construction: After mating, the female proceeded to make a slanting tunnel which terminated in a brood chamber. The ball was torn apart and refashioned into a pear shaped ball. An egg was laid in the egg chamber constructed at the top end of this fashioned brood ball. The ball rested on its broad end in a pear shaped brood chamber located at an average depth, of 5.1 cm (*G. gemmatus*) and 7.5 cm (*G. miliaris*). The average length and breadth of the brood balls of *G. miliaris* and *G. gemmatus* were 1.45 ± 0.23 cm and 1.2 ± 0.18 cm (n = 12); and 1.34 ± 0.31 cm and 1.1 ± 0.08 cm (n = 10), respectively. Their respective weights were 1.12 ± 0.2 g (n = 12) and 0.99 ± 0.18 g (n = 10).

Competition: Both the species of *Gymnopleurus* under review exhibited inter- and intra-specific competition.

Intra-specific competition: There was intense competition among the males to gain possession of ready made dung balls. This was observed from the very first day of activity.

Ball rolling males had to repeatedly fend off males that challenged the right to ownership of their ball. On sensing the arrival of a rival, the owner stood on the ball with its head towards the ground. The strategy of the rival male was always to move around

the ball trying to get a foot hold. The owner of the ball would keep moving on the ball so that the rival was always on the ground without access to the ball. If the rival came too close, the owner tossed it away using its clypeus. But if the rival managed to out manouvre the owner and get atop the ball, then it in turn would toss the owner away.

Whenever a rolling pair was challenged by the arrival of a rival male it was only the male that fought him while the female remained passive. They butt and toss each other in combat. If the period of waiting was too long the female abandoned the fighting males with the ball, in search of a new partner.

Whenever a pair of rollers were rolling a ball, they were followed by males of their own species as well as other species. The males followed the ball either by walking or flying. Whenever the pair stopped rolling, the male that was following behind hid under grass or leaves in the vicinity. In this way, males followed the ball till the pair started burying the ball. Then the males in hiding attempted to reach the digging female, but retreated whenever the 'owner' male noticed and chased them. It was also observed that when the owner male succeeded in getting at the smaller intruder males, he sat atop them and started drumming on them with his clypeus and forelegs after which the looser ran away and took cover in the grass.

It was also noticed that whenever a male sitting and waiting on a ball, saw another male sitting or rolling a ball nearby it immediately chased the other male and took possession of that ball. In one such case a male took poosession of new balls on three successive occasions.

Competition was seen even after the ball was buried. Males of *G. miliaris* and *G. gemmatus* were seen landing and walking straight into mounds of soil where pairs of *G. miliaris* and *G. gemmatus* were found with dung balls. Males of one species sneaked into the burrows of other species.

Interspecific combat: Various species of *Onthophagus* and *Caccobius* also compete for access to dung balls in addition to the competition that has been noticed between the two species of the *Gymnopleurus* under study. Three species of *Onthophagus*, namely *O. centricornis*. *O. pygmaeus* and *O. ludio* Bouc. and one species of *Caccobius*, namely *C. meridionalis* Bouc., tried repeatedly to gain entry into the brood balls of both *G. miliaris* and *G. gemmatus*.

Competition was noticed between the males of *G. miliaris* and *G. gemmatus* for the balls, and was similar to that explained in intraspecific competition. In one instance combat was observed between two females of *Gymnopleurus* spp. for the ball. The ball was pulled out by *G. gemmatus* and during the process of combat the ball was being rolled along.

The presence of kleptoparasites was noticed right from the ball construction stage to even after the egg had been laid in the brood ball. But they proved to be more persistent attackers once the beetles commenced rolling the balls. The kleptoparasites followed the rolling pairs on the wing, alighted in the vicinity of the ball and sought a hasty entry into it whenever the pairs paused for some reason. One pair of *G. miliaris* that was observed, had to face attacks from *G. gemmatus* (once), *O. centricornis* (eleven times), *O. pygmaeus* (four times) and *O. ludio* (once), while having to traverse a distance of 17.10 m.

If detected the *Gymnopleurus* spp. butted and tossed away the sneaking kleptoparasitic species. Even those kleptoparasites that had managed to enter the ball unnoticed were detected in a short while and extricated from the ball after it had been pried open by *Gymnopleurus*. Along with the kleptoparasite a small amount of dung was lost. The ball was then refashioned once more and the process of rolling continued.

It was also noticed that those males with the ball abandoned by the female never extricated the kleptoparasites when they entered the ball but flew away abandoning them.

The kleptoparasites that escape detection convert the brood balls of *Gymnopleurus* into brood masses for their own off-spring, *O. centricornis* was observed to have made four brood masses out of one brood ball in one instance. In two other cases they had converted it into 2 or 3 brood masses. In the

latter case the brood masses weighed 160, 110 and 118 mg.

Predation: Analysis of the stomach contents of the garden lizard *Calotes* sp. revealed fragments of *Gymnopleurus.*

Ants of the genus *Camponotus* were also found attacking ball rolling individuals of *G. gemmatus.* When attacked, the beetles abandoned the balls and flew away.

G. gemmatus and *G. miliaris* invest a considerable quantum of their time and energy in the fashioning (11.08 ± 1.36 min., 10.40 ± 1.14 min. respectively) and burial (14.36 ± 3.66 min.; 13.45 ± 2.8 min. respectively) of dung balls. The evolution of this behaviour not only enables these species, like the other dung rollers, to rapidly acquire the necessary resources in ball form, but it also provides the females ample opportunity to choose a more fit male. Hence, while giving these species an edge in the competition for food and burial space over the other burying groups like the Coprini, Onthophagini, etc., which are competing beneath or around each dung pat (Halffter and Matthews 1966) this behaviour simultaneously ensures rigorous epigamic selection (Huxley 1938). However, the greater amount of time spent on the surface of the ground while rolling exposes these beetles to the hazards of parasitism and predation.

Observations made during the current study indicate that while pre-mating female choice does occur in both the species, female choice during and after mating are also possible.

Pre-mating female choice occurs during the three stages of fashioning, transportation and burial of the ball.

i. **Ball fashioning**: To increase their reproductive success by attracting females, males of *G. miliaris* and *G. gemmatus* have to fashion relatively larger balls of excrement. As there is very low correlation between the size of the male and the size of the female (r=0.08) the female does not seem to be choosing males. The weak correlation between the male size and ball size indicates that large individual size does not necessarily result in large ball size (r=0.2). All this combined with the fact that female size and ball size are relatively highly correlated (r=0.57) points to the possibility of cryptic female choice (Fig. 1).

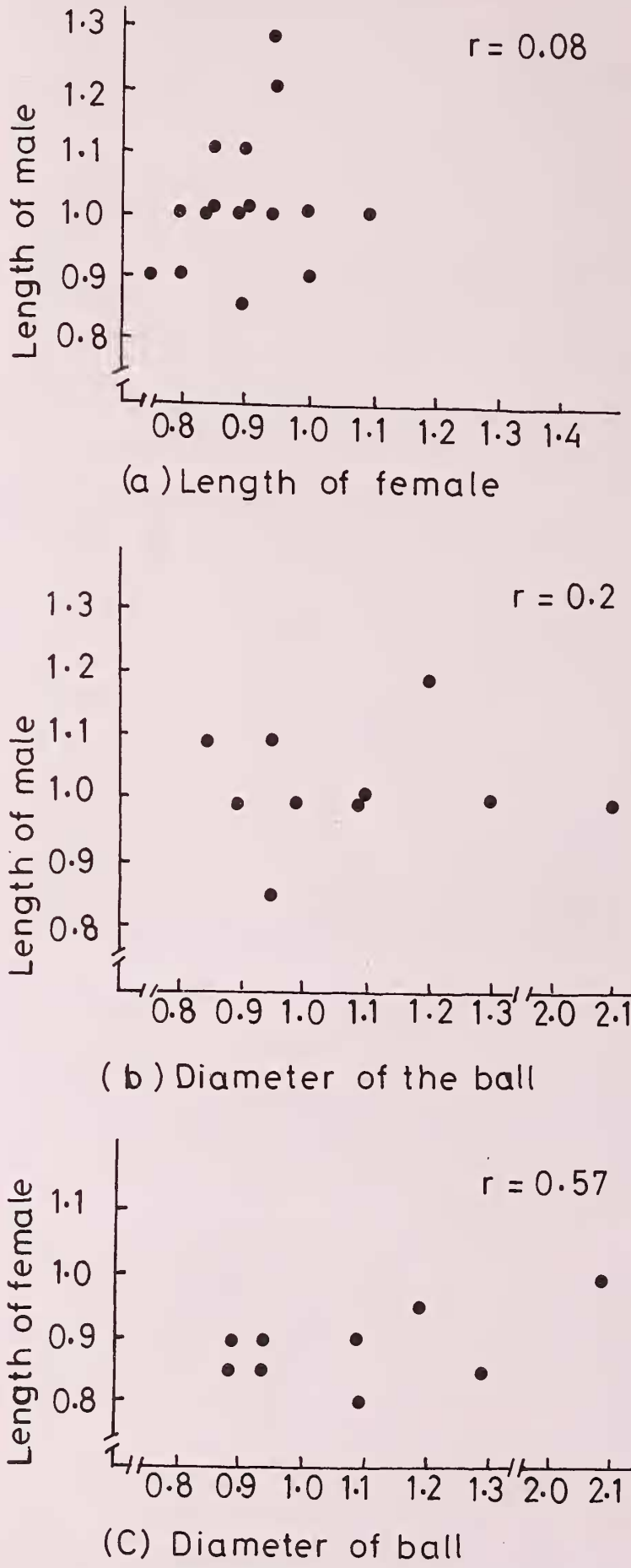

Fig. 1. Relationship between length (cm) of (a) male and female; (b) male and dung ball (dia.); (c) female and dung ball (dia.) in *G. miliaris.*

Instead of choosing the larger males (r=0.08) females are choosing larger balls (r=0.57).

ii) **Ball transportation**: Having initially chosen a male capable of making a larger ball, the female further assesses male capability/fitness by:

a) watching how soon the male she has chosen can ward off the intruder males; b) choosing the winning male in the event of a skirmish. Males which take either too long to win a fight or are ousted in battle are abandoned by the females.

iii) **Ball burial**: In this phase males face the danger of losing females to other competing males or to having their effort wasted by intruding kleptoparasites which occupy the dung balls and destroy the eggs of *Gymnopleurus*. Intraspecific male competition is thus intense during these phases.

iv) **Mating**: During mating the female can exercise mate choice by regulating the mating duration. However, since the number of mating individuals observed during the study was small (n = 4 for *G. gemmatus,* for *G. miliaris* n = 5) no definite conclusions could be arrived at in this regard (cv for *G. gemmatus* was 16.6, while for *G. miliaris* it was 21.7).

v) **Post-mating**: The female makes her final choice of the male by deciding whether to mate again or not. Having mated once, females have been observed to mate again. The presence of a horse-shoe shaped spermatheca also points to the distinct possibility of sperm precedence (Halffter and Edmonds 1982) as the sperm of the last mated male is most likely to fertilize the ova in spermatheca shaped thus. This could be the reason for the male to follow rolling bisexual pairs, waiting for an opportunity to be the final one to copulate with a female before she lays eggs.

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